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Aboveground productivity and root–shoot allocation differ between native and introduced grass species

Brian J. Wilsey · H. Wayne Polley

Abstract Plant species in grasslands are often separated into groups (C_4 and C_3 grasses, and forbs) with presumed links to ecosystem functioning. Each of these in turn can be separated into native and introduced (i.e., exotic) species. Although numerous studies have compared plant traits between the traditional groups of grasses and forbs, fewer have compared native versus introduced species. Introduced grass species, which were often introduced to prevent erosion or to improve grazing opportunities, have become common or even dominant species in grasslands. By virtue of their abundances, introduced species may alter ecosystems if they differ from natives in growth and allocation patterns. Introduced grasses were probably selected nonrandomly from the source population for forage (aboveground) productivity. Based on this expectation, aboveground production is predicted to be greater and root mass fraction to be smaller in introduced than native species. We compared root and shoot distribution and tissue quality between introduced and native C_4 grass species in the Blackland Prairie region of Central Texas, USA, and then compared differences to the more well-studied divergence between C_4 grasses and forbs. Comparisons were made in experimental monocultures planted with equal-sized transplants on a common soil type and at the same density. Aboveground productivity and C:N ratios were higher, on average, in native grasses than in native forbs, as expected. Native and introduced grasses had comparable amounts of shallow root biomass and tissue C:N ratios. However, aboveground productivity and total N were lower and deep root biomass and root mass fraction were greater in native than introduced grasses. These differences in average biomass distribution and N could be important to ecosystems in cases where native and introduced grasses have been exchanged. Our results indicate that native–introduced status may be important when interpreting species effects on grassland processes like productivity and plant N accumulation.

Keywords Invasive species · Introduced species · Exotic species · Grasslands · Root biomass · Tallgrass prairie · Texas

B. J. Wilsey (✉)
Department of Ecology, Evolution and Organismal Biology,
253 Bessey Hall, Iowa State University,
Ames, IA 50011, USA
e-mail: bwilsey@iastate.edu

H. Wayne Polley
USDA-ARS, Grassland, Soil and Water Research
Laboratory, Temple, TX 76502, USA

Introduction

Because species composition can vary enormously from place to place, it has become common to group species into functional groups in order to generalize across sites and studies. For example, grassland species are usually classified into functional groups based on their mode of photosynthesis (C_4 or C_3), their growth form and taxonomy (e.g., grass-like graminoids or broad-leafed forbs), or their ability to harbor N-fixing bacteria (legumes or nonlegumes). Species (or functional group) composition has been found to be an

important predictor of primary productivity, nutrient cycling, and decomposition rates (e.g., Wedin and Tilman 1990; Chapin et al. 1996). Species (or functional group) composition alone explained as much or more of the variation in productivity as species richness (reviewed by Loreau et al. 2001 and Hooper et al. 2005) or evenness (Wilsey and Potvin 2000; Polley et al. 2003) in tests of biodiversity–productivity relationships.

Another way of grouping species that is potentially important to ecosystem functioning is according to their native–introduced status (Vitousek 1990, 1994; Baruch and Goldstein 1999; Richardson et al. 2000; Ehrenfeld 2003; D'Antonio and Hobbie 2005; Reed et al. 2005). In grasslands of North America, many introduced species have spread after their introduction to become common or even the dominant species. For example, the grasses *Bromus inermis* (smooth brome) and *Agropyron cristatum* (crested wheatgrass) are dominant grasses in much of the Northern Plains region (e.g., Christian and Wilson 1999; Cully et al. 2003), introduced species of the genus *Agropyron* (now *Pseudogneria*) or *Centaurea* dominate some intermountain grasslands (Caldwell et al. 1981; Richards 1984; Pyke 1990; Callaway and Aschehoug 2000; Callaway et al. 2004), introduced annuals dominate California grasslands (e.g., Seabloom et al. 2003), and the grass *Bothriochloa ischaemum* (KR Bluestem) dominates many central Texas grasslands (Wilsey and Polley et al. 2003). These species have spread rapidly. For example, Correll and Johnston (1979) stated in the Flora of Texas that *Bothriochloa ischaemum* was "not persisting except in cultivation or along roadsides."

The spread of introduced species and the potential homogenization of flora has become a global issue (Vitousek 1994; Wilcove et al. 1998; Levine and D'Antonio 1999; Olden and Poff 2003), yet we have few experimental tests of whether introduced species differ from natives in traits that affect community and ecosystem processes (Baruch and Goldstein 1999; Smith and Knapp 2001; Ehrenfeld 2003). Vitousek (1990) proposed that introduced species could impact ecosystem processes if they: (1) acquire and use resources differently from native species, (2) alter trophic relationships, or (3) change the frequency or intensity of disturbance. Introduced species can also affect ecosystem processes through changes in plant–soil organism feedbacks (e.g., Ehrenfeld et al. 2001; Evans et al. 2001). In this paper, we focus on the first of these processes: whether resources are used differently between introduced species and natives. The idea that introduced species are drivers of change in plant diversity (which is widely accepted, but infrequently tested)

implies that introduced species differ from natives in traits associated with resource uptake that ultimately determine the outcome of plant–plant interactions.

There is currently no strong consensus on whether introduced species differ from natives in their aboveground growth rates, and characteristics based on belowground growth are especially poorly understood. Ehrenfeld (2003) found that net primary productivity and standing crop biomass were higher in invaded sites in 14 out of 18 cases she reviewed. In two other recent review articles, Vilá and Wiener (2004) found greater aboveground growth rates in natives than introduced species, whereas Daehler (2003) found that there was no consistent difference between natives and introduced species. A potential problem with many published comparisons is that they do not replicate species within each introduced or native group, and the lack of replication may have been responsible for the lack of a significant difference in the review of Daehler (2003), which was based on a tally of results as native > exotic, native = exotic, or native < exotic. Wilsey (2005) found that only 16% of studies in which native and introduced species were compared included replication, and that conclusions about exotic–native differences varied between replicated and unreplicated data sets. Paired species (i.e., one native and one introduced species) studies are directly relevant only in ecosystems where monocultures are common, such as salt marshes (e.g., Callaway and Josselyn 1992). They are much less directly relevant to ecosystems like grasslands where multiple species interact at small spatial scales. In these systems, a lack of species replication is problematic for developing general predictions on how introductions impact ecosystems, because large variation among species within native or introduced species groups may obscure average differences between groups (Wilsey 2005). This problem can be circumvented by replicating introduced and native species in comparative studies (Baruch and Goldstein 1999; Smith and Knapp 2001). Furthermore, very little data exist on belowground differences between native and introduced species, with only a few studies including root data (e.g., refer to the data set collected by Daehler 2003). This is because of the great difficulty in differentiating roots among species in mixed stands.

Most introduced grass species were intentionally introduced to reduce erosion or to improve grazing opportunities. Consequently, these species were probably selected by humans for forage (aboveground) productivity and N accumulation. This human selection could have occurred either with or without enemy release. Thus, we predict that aboveground production and N accumulation are greater and root mass fraction

is smaller in introduced than in native species. To test this hypothesis, we compared differences in root and shoot biomass and tissue quality between introduced and native C_4 grass species grown in experimental monocultures with differences observed between native C_4 grass and forb species. Experimental comparisons such as these have the advantage of avoiding confounding factors that can complicate observational and comparative studies [i.e., whether introduced species are the drivers or passengers of ecosystem change (McDougal and Turkington 2005)]. For example, 70% of the studies reviewed by Ehrenfeld (2003) were based on observational studies of invaded versus uninvaded sites. In these cases, confounding variables may be present due to the nonrandom nature of invasion (Levine and D'Antonio 1999; McDougal and Turkington 2005). However, manipulative experiments have the disadvantage of disturbing soil during plot establishment (D'Antonio and Hobbie 2005). This disturbance is less of an issue if the study species establish with disturbance, as they do in our case. By comparing plots with only a single species present, we are able to measure root biomass by species.

Methods

Experimental design and study area

Our objectives were addressed in an experiment conducted at the Grassland, Soil and Water Research Laboratory in the Blackland Prairie region of Central Texas on a vertisol soil. The climate of the area is subhumid, with an average of 864 mm of precipitation per year. The Texas Blackland Prairie region, which was formerly tallgrass prairie (Risser et al. 1981), contains about 50% formerly cropped grasslands that have become dominated by introduced grasses, as well as a few scattered grasslands dominated by native species (Wilsey and Polley 2003). A full description of our experimental design, which included plots that varied in species richness and evenness, is included in Wilsey and Polley (2004). Briefly, we planted 75 plots 1 × 1 m in area with 96 small equally sized seedlings that were propagated in field soil in 4 in. pots before planting them in mid-April 2001. Thirteen species were used in our study, and each species was planted into three monoculture plots (39 monocultures total). However, we based the analysis on 11 of 13 species for reasons explained below. Treatments were randomly assigned within three blocks, each with 13 monoculture plots.

The 13 species used in this experiment were selected because they are the most frequently found perennial

species within grasslands of the region. Wilsey and Polley (2003) sampled a nearby prairie remnant and found that C_4 grasses provide approximately 69% of the net aboveground primary productivity, with annual and perennial forbs at 28%, C_3 grasses 2%, and legumes 1%. In grasslands dominated by introduced species, 66 and 21% of net primary productivity consisted of C_4 and C_3 grasses. Five of the species that we studied are native C_4 grasses: *Schizachyrium scoparium* (Michx.) Nash, *Sporobolus compositus* (Poir.) Merr. (formerly *asper*), *Bothriochloa laguroides* (DC.) Herter, *Bouteloua curtipendula* (Michx.) Torr, and *Sorghastrum nutans* (L.) Nash. Three are introduced C_4 grasses: *Bothriochloa ischaemum* (L.) Keng, *Paspalum dilatatum* Poir, and *Panicum coloratum* L. Four species are native C_3 forbs: *Ratibida columnifera* (Nutt.) Wooton & Standl, *Oenothera speciosa* Nutt, *Salvia azurea* Michx. ex Lam, and *Echinacea purpurea* (L.) Moench (nomenclature follows Diggs et al. 1999). Thus, we replicated native and introduced C_4 grasses and native forbs for comparisons. We did not include introduced perennial forbs because none are common to the area. We also planted the one common C_3 grass in our area, *Nasella* (formerly *Stipa*) *leucotricha*, but it was not included here because species were not replicated within the C_3 grass group. *Oenothera speciosa* died following the first year (possibly as a result of a beetle outbreak) and was excluded from our analysis.

Response variables

Aboveground productivity was estimated with peak biomass, which was collected in October of each year by clipping all plants to 2 cm in height. Peak biomass underestimates net primary productivity, but is a good comparative estimate of net aboveground productivity in this system because frost kills aboveground biomass during the winter and there is no carryover of biomass from year to year. Root biomass was estimated by extracting roots from soil cores. Root biomass carried over from year 1 to year 2, so it is more appropriate to call root biomass "peak biomass" rather than productivity.

Roots were extracted from a 4.2 cm diameter soil core removed from each plot during fall of year 1 (2001). Two cores per plot were collected in year 2 (2002). Each core was sectioned into an upper "shallow" (<20 cm) and lower "deep" (20–45 cm) layer to examine differences in rooting distribution. Cores were collected to 45 cm because most roots are found in this layer of soil (Jackson et al. 1996). Virtually every root observed was alive at sampling (personal observation). Live roots were hand-picked from cores and were then

washed over a 0.5 mm screen. Root mass fraction (RMF) was calculated as (shallow + deep roots)/ (shallow + deep roots) + shoot biomass, with all variables scaled to a 1×1 m area. Root mass fraction is conceptually similar to root–shoot ratio, but it has desirable statistical properties because it compares root biomass to total plant size.

Aboveground biomass samples were ground through a Wiley mill and analyzed for C and N content with a CE Elantech (Lakewood, NJ, USA) Flash EA1112 combustion C:N analyzer. The proportion of N was then multiplied by the biomass to obtain estimates of total aboveground N. Total aboveground N is a measure of N accumulation by the aboveground biomass during the current growing season.

Statistical analyses

Aboveground, shallow and deep-root biomass and root mass fraction were analyzed with randomized block, nested repeated measures multivariate (MANOVA) and univariate analyses of variances (ANOVA) using PROC GLM of SAS 8.1 (Littell et al. 2002). Both functional groups and species nested with functional groups were considered as fixed effects (Neter et al. 1996, pp 1127–1132). A fixed-effects model was used because all major perennial species from the area were used rather than a random sample of species from a larger species pool. MANOVA is appropriate when variables are moderately correlated (Stevens 1986) because it takes into account correlations among variables when comparing among groups (Littell et al. 2002). Correlations among variables in year 1 ranged from $r=0.10$ between deep-root biomass and root mass fraction to $r=-0.73$ between aboveground biomass and root mass fraction. In year 2, they ranged from $r=0.08$ to 0.15 between shallow and deep root biomass and aboveground biomass, respectively, to -0.68 between aboveground biomass and root mass fraction. When MANOVA terms were significant, univariate ANOVA was then considered. A priori contrasts were made between grouped native and introduced C_4 grass species, and between grouped native C_4 grasses and native C_4 forbs. An alternative method of analyzing data using one-way models of species effects ($n=11$), along with a priori contrasts of groups gave results similar to those presented here. All variables were normally distributed (Wilks W, all P values >0.1), but biomass variables were *ln*-transformed, and RMF was arcsin($\sqrt{}$) transformed to minimize heteroscedasticity.

Tissue quality variables were measured in year 1 only, so they were analyzed with a randomized block ANOVA with the same contrast statements as described above. However, because aboveground biomass and total aboveground N gave nearly identical results ($r=0.89$, $P<0.001$, $n=33$), we analyzed biomass alone as a surrogate for both variables.

Results

Differences between native and introduced C_4 grasses

Introduced grass species differed from native species in biomass and allocation variables (i.e., the introduced grass versus native grass contrast from the MANOVA was significant, Table 1). The amount of difference between these groups was consistent across the two years for all variables except aboveground biomass (i.e., year × contrast interaction in MANOVA was significant, Table 1).

Differences in mean peak aboveground and deep-root biomass were opposite in direction between introduced and native grass groups. In year 1, peak aboveground biomass was greater on average by a factor of 2 for introduced (mean of 1.21 kg/m^2) than for native grasses (mean of 0.60 kg/m^2) (Fig. 1a, Table 1). In year 2, it was greater by a factor of 1.6 (means, introduced: 0.74 kg/m^2, native: 0.45 kg/m^2). Total aboveground N gave results very similar to biomass, with introduced species having a mean of 7.3 g N/m^2 and natives a mean of 4.0 g N/m^2 (Fig. 1b). Biomass of shallow roots did not differ between introduced and native grasses (Fig. 2a, Table 1), but biomass of deep roots was about two times greater for native than introduced grasses (means of 78.5 and 128.0 g/m^2 in years 1 and 2 for natives and of 42.8 and 68.3 g/m^2 for introduced species, Table 1) (Fig. 2b). As a result of these differences in peak aboveground and deep-root biomass, the proportion of biomass allocated to roots (RMF) was greater on average in native grasses (means: 0.51 in year 1, 0.69 in year 2) than introduced grasses (means: 0.36 in year 1, 0.50 in year 2) (Fig. 3). However, C:N ratio of aboveground tissues did not differ between native (mean of 64.2) and introduced (mean of 63.9) C_4 grass species (introduced grass vs. native grass contrast, $F_{(1,20)}=0.01$, P value >0.9, Table 2).

Differences between native C_4 grasses and forbs

Native C_4 grass species as a group also differed from forb species in biomass and allocation (i.e, the native forb vs. native grass contrast from MANOVA was significant, Table 1). The amount of difference between these groups was consistent across the two years for all

Table 1 Results from repeated measures MANOVA (numerator and denominator *df* and *F*) and ANOVA (*df*, mean square (MS) and *F*) for biomass and root-mass ratio among groups [native C_4 grasses (N), introduced C_4 grasses (I), or native forbs (F)], between introduced and native C_4 grasses (I vs. N contrast), between native C_4 grasses and forbs (N vs. F contrast), and among species within groups

Effect	MANOVA		ANOVA								
			Above			Shallow roots[b]		Deep roots[c]		RMF	
	df,df[a]	F	df	MS	F	M S	F	MS	F	MS	F
Block	8,34	1.3	2	0.00	0.4	0.1	0.1	0.3	0.5	0.00	0.1
Group	8,34	14.3***	2	6.8	80.0***	0.7	1.4	5.6	10.2***	0.23	10.6***
I versus N	4,17	12.8***	1	4.2	49.9***	0.0	0.1	3.4	6.3*	0.34	15.8***
N versus F	4,17	15.3***	1	4.2	50.0***	1.4	2.7	10.7	19.5***	0.01	0.5
Species (group)	32,64.3	5.0***	8	2.0	23.9***	1.4	2.7*	0.7	1.4	0.09	4.1**
Error			20	0.08		0.52		0.55		0.02	
Year	4,17	11.8***	1	0.3	25.2***	2.8	7.2*	5.9	17.5***	0.23	20.2***
Year × block	8,34	1.5	2	0.1	5.9**	0.1	0.3	0.0	0.1	0.00	0.1
Year × group	8,34	12.4***	2	1.0	89.0***	0.0	0.1	0.0	0.1	0.03	2.9†
Year × S (G)	32,64	2.6***	2	0.1	9.6***	0.6	1.6	0.5	1.5	0.02	2.0†
I versus N	4,17	3.4*	1	0.1	5.5*	0.0	0.1	0.0	0.0	0.00	0.4
N versus F	4,17	28.6***	1	1.5	127.7***	0.1	0.1	0.0	0.2	0.06	5.8*
Error			20	0.01		0.39		0.33		0.01	

[a] Wilk's Lambda

[b] 0–20 cm depth

[c] 20–45 cm depth

† $0.05 < P < 0.1$, * $0.01 < P < 0.05$, ** $0.001 < P < 0.01$, *** $P < 0.001$

variables except aboveground biomass and root mass fraction (i.e., year × contrast interaction in MANOVA was significant, Table 1).

On average, aboveground peak biomass and deep-root biomass were greater for native grasses than for forbs (Fig. 1, 2). Aboveground peak biomass was 2.6-fold higher in grasses (mean 694.8) than forbs (272.4) in year 1, and 1.2-fold higher in year 2 (523.6 for grasses vs. 425.8 for forbs). Shallow root biomass did not differ between grasses and forbs. Deep roots were higher for native grasses (year 1: 78.7 g/m², year 2: 128.0 g/m²) than for forbs (year 1: 33.8 g/m², year 2: 51.9 g/m²). Root mass fraction was greater for native forbs (0.62) than for native grasses (0.51) during year 1 (time × forb vs. grass contrast, $P=0.037$) but was similar during year 2 (0.64 vs. 0.69). Native forbs had lower average C:N ratios (forb vs. grass contrast, $F_{(1,20)}=17.9$, $P<0.01$, mean of 51.5) than did native grasses (64.2) (Table 2).

Variation among species within groups

We also found significant variation among species within functional groups for all variables except deep-root biomass [MANOVA: species (functional group) effect, Table 1]. These differences were consistent across years for all variables except aboveground biomass, which varied slightly more in year 2 than year 1.

Discussion

We found differences in biomass production and distribution between native and introduced C_4 grasses that were as great as the differences between grasses and forbs. Differences between grasses and forbs have been reported previously and are fairly well-understood (e.g., Tjoelker et al. 2005, Polley et al. 2002). At our study site, Polley et al. (2002) found that perennial forbs had higher tissue N contents and differed in plant water status from the perennial grass *Bothriochloa ischaemum*. The greater productivity of C_4 grasses compared to native forbs was especially apparent in our system, where relatively high mean annual temperatures favor C_4 over C_3 photosynthesis. However, the observed differences between native and introduced C_4 grasses in their growth and allocation patterns was surprising to us and could impact important ecosystem and community-level processes in addition to the ones (productivity and N uptake) documented here. Introduced grasses had much higher aboveground productivity and N uptake, lower allocation to roots, and lower deep-root biomass than did native grasses. It is important to note that these introduced grasses are common or even the dominant species in their native ranges and are not merely early successional species (Sims and Dewald 1982; McNaughton 1983; Soriano 1991; Loreti 2001). Furthermore, in contrast to the results of Wedin and Tilman (1996); Baruch and
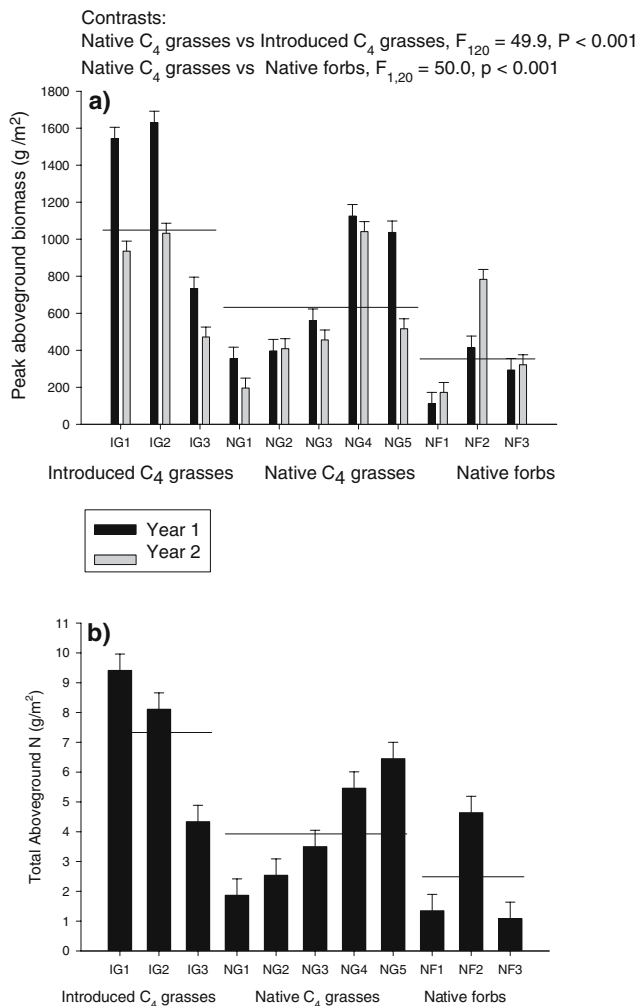
Fig. 1a–b Peak aboveground biomass (**a**) and total aboveground (**b**) N (+SE) in three introduced C_4 grass (IG), five native C_4 grass (NG), and three native forb (NF) species. Species are as follows : *IG1 Bothriochloa ischaemum, IG2 Panicum coloratum, IG3 Paspalum dilatatum, NG1 Schizachyrium scoparium, NG2 Sorghastrum nutans, NG3 Bouteloua curtipendula, NG4: Bothriochloa laguroides, NG5: Sporobolus asper, NF1: Echinacea purpurea, NF2: Ratibida columnifera, NF3: Salvia azurea.* Contrast results are from a priori contrasts that decompose the species treatment into tests comparing introduced and native C_4 grasses as well as native C_4 grasses and native C_3 forbs. *Horizontal lines* indicate the approximate locations of two-year group means

Fig. 2a–b Shallow (0–20 cm) (**a**) and deep (20–45 cm) (**b**) roots among three introduced C_4 grasses (IG), five native C_4 grasses (NG), and three native forb (NF) species. Abbreviations are the same as in the legend for Fig. 1. *Horizontal lines* indicate the approximate locations of two-year group means. Notice the difference in scale between **a** and **b**

Goldstein (1999) and Craine and Lee (2003), the native and introduced species we studied did not differ in tissue quality.

Although introduced and native grasses differed in patterns of peak aboveground and deep-root biomass, it is important to emphasize that large differences among species were unaccounted for by native–introduced or grass–forb groupings (in all variables except deep-root biomass). For example, the native species *Bothriochloa laguroides* tended to have high above-
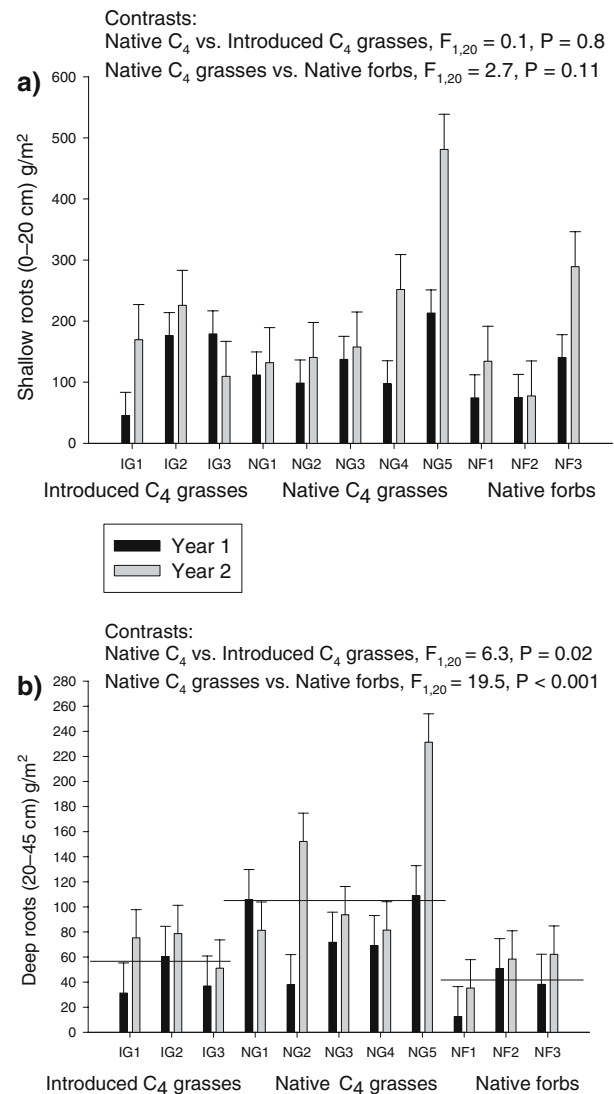
ground productivity that was more typical of the introduced species (Fig. 1a). Anderson and Briske (1999) found that this species is more abundant in heavily than in lightly grazed grasslands, and it is largely absent from intact prairies. This species has been characterized as a "weedy" grass (Hatch and Pluhar 1993) with a wide distribution from the southern US to South America (Soriano 1991). Species composition is consistently found to be important in experiments of biodiversity and ecosystem functioning, where species (or functional group) composition can explain as much or more of the variation in productivity as species diver-
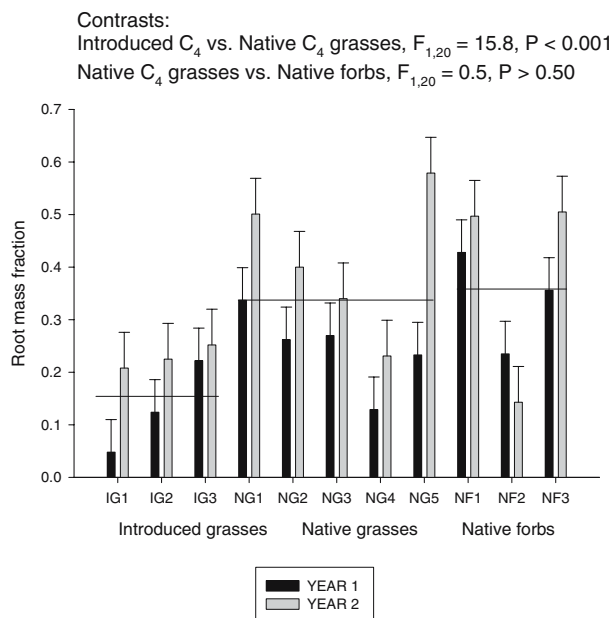
Contrasts:
Introduced C_4 vs. Native C_4 grasses, $F_{1,20} = 15.8$, $P < 0.001$
Native C_4 grasses vs. Native forbs, $F_{1,20} = 0.5$, $P > 0.50$

Fig. 3 Root mass fractions among three introduced C_4 grasses (IG), five native C_4 grasses (NG), and three native forb (NF) species. Abbreviations are the same as in the legend for Fig. 1. *Horizontal lines* indicate the approximate locations of two-year group means

Table 2 Species used in the study, and their least-square mean C:N ratios in monoculture plots grown under a common soil type and with common densities

Species	C:N ratio
Native C_4 grasses	
Schizachyrium scoparium	70.3
Sporobolus asper	61.2
Bothriochloa laguroides	74.2
Bouteloua curtipendula	55.2
Sorghastrum nutans	60.3
Mean	64.2
Introduced C_4 grasses	
Bothriochloa ischaemum	60.5
Paspalum dilatatum	55.6
Panicum coloratum	75.6
Mean	63.9
Native C_3 forbs	
Ratibida columnifera	30.8
Salvia azurea	98.9
Echinacea purpurea	24.7
Mean	51.5
LS mean standard error	4.1

sity (reviewed by Loreau et al. 2001 and Hooper et al. 2005).

Variation among species within groups can also complicate interpretation of paired species experiments, where different outcomes (e.g., native > introduced, native = introduced, or native < introduced) are possible between pairs solely due to the variation

among species within each group (Wilsey 2005). For example, Wilsey (2005) reanalyzed the data presented by Daehler (2003) and found that in replicated studies aboveground biomass was higher for introduced than for native species much more frequently than in nonreplicated studies (Wilsey 2005). In this study, if we had chosen *Bothriochloa laguroides* by chance to be our native species for comparisons with the introduced species *Paspalum dilatatum*, we would have reached a conclusion about differences between native and introduced species that was opposite to that observed between group means (Wilsey 2005). This suggests that results from studies in which species are replicated will be less variable than those studies of a pair of species.

The introduced species studied here were introduced primarily to improve grazing opportunities, and we hypothesize that higher average aboveground productivity (i.e., forage production) and N accumulation were probably targeted by people who introduced them (Caldwell et al. 1981; Simose and Baruch 1991). One of the most common introduced species in the Blackland Prairie region, *Bothriochloa ischaemum*, was introduced from China in 1917 to reclaim marginal farmland and was later planted along roadsides (Sims and Dewald 1982; Diggs et al. 1999). Since then, it has spread into both ungrazed and grazed areas. The other two introduced grasses are common in Africa (*Panicum coloratum*) and South America (*Paspalum dilatatum*), respectively (McNaughton 1983; Soriano 1991; Loreti et al. 2001). In these cases, and perhaps in any case where species were intentionally introduced, we suggest that there was human selection for certain characteristics that matched the objectives of the initial introduction. This human selection may have resulted in higher average aboveground biomass in introduced species that may be independent of, or in addition to, any possible enemy release effects. In the case of these introduced forage species, the enhanced aboveground productivity may have made them attractive candidates for improving grazing opportunities (Sims and Dewald 1982), but their lower root mass fraction and lower deep-root biomass may be having unanticipated effects on belowground processes.

Our results are largely consistent with the hypothesis of Ehrenfeld (2003) that introduced species have lower root–shoot ratios (root mass fraction). Ehrenfeld (2003) reviewed six studies that compared root–shoot ratio, five of which supported her conclusion that root–shoot ratios are lower in invasive species. However, all of these studies had variables that covaried with invasive species abundance, such as disturbance (Rutherford et al. 1986, Versfeld and van Wilgren 1986, Bolton et al. 1993) or annual–perennial status (Holmes and

Rice 1996). Here, we provide the first experimental support for the hypothesis by Ehrenfeld (2003) that introduced species have lower root–shoot ratios (in our case, root mass fraction) on average than do native species under common environmental conditions.

The finding that native grass species have twice the deep-root biomass of introduced species has potentially important implications for ecosystem processes in lands that have been converted to introduced grass dominance or that, conversely, have been restored back to native species dominance. Our results suggest that grasslands dominated by introduced species in our region have a greater flow of energy through the aboveground pathway and less flowing to the deeper soil layer. Restoring native species could reverse this pattern. A greater proportion of roots in deeper soil layers may lead to increased drought or frost resistance (Schenk and Jackson 2002), micronutrient uptake (McCulley et al. 2004), and in the longer term, to increased soil C storage (Nepstad et al. 1994, Gill and Burke 2002). These effects may become apparent over a longer time frame (e.g., a decade time frame) than we looked at here. For example, greater biomass at deeper rooting depths was found mainly in water-limited systems (Schenk and Jackson 2002), suggesting a relationship between these two variables. The deeper soil layers are especially important to soil C storage because the rate of root decomposition decreases with depth (Gill and Burke 2002). Although root production also declines precipitously with depth, soil C declines at a much lesser rate (Gill and Burke 2002) such that the ratio of soil C to biomass is greater in deeper than in shallow soil layers (Weaver et al. 1935, Gill et al. 1999). For example, Weaver et al. (1935) found that ~60% of roots but only 17–32% of soil C was found in the top 15 cm of soil in tallgrass prairies in eastern Nebraska and western Iowa. Comparable estimates for short grass steppe in Colorado are 66% roots: 34% soil C in the upper 10 cm (Gill et al. 1999). The deeper roots of native grasses are more likely to enter C pools with longer residence times, which may lead to increased C storage after many growing seasons. Plots will be sampled in future years to test this hypothesis. Christian and Wilson (1999) found that Canadian fields planted 50 years earlier with the introduced grass *Agropyron cristatum* had lower soil C and N contents than did native-dominated successional prairies that were not planted with this species.

These differences between native and introduced grass species, as well as their responses in mixture (Polley et al. 2003; Wilsey and Polley 2004), should be taken into account in future studies. Introduced grass species can suppress forest development (e.g., Hooper

et al. 2004), reduce species diversity (e.g., Christian and Wilson 1999), affect N cycling and fire regimes (e.g., D'Antonio and Vitousek 1992; Platt and Grottschalk 2001; Reed et al. 2005), increase soil C sequestration when properly managed (Fisher et al. 1994), and have different biomass distributions, on average, compared to native grass species (this study). We studied just eight native and introduced species from a single region in North America with a fixed-effects experimental design, so studies in which native and introduced species are replicated under comparable conditions (e.g., common soil type, age, and planting density) are required at other sites. Nevertheless, our results indicate that the native–introduced status of plant species may be important in interpreting species effects on grassland processes like productivity and plant N accumulation.

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